LONG-TERM ECOLOGICAL CONSEQUENCES OF VARYING FIRE FREQUENCY IN A HUMID GRASSLAND

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ABSTRACT

The ecological consequences of different fire frequencies imposed for 20 years in an eastern Kansas grassland were evaluated with particular emphasis on responses in plant species richness and aboveground net primary production (ANPP). Pre- and postfire data from several burns across a variety of sites indicated that species richness in tallgrass prairie was not significantly impacted by an individual fire. However, long-term records from sites burned: (1) annually, (2) an average of once-in-4 years and (3) once-in-14 years, clearly showed that annual fire decreases species richness, whereas infrequent fire may enhance the total number of species present. A long-term record is also necessary to adequately assess ANPP responses to fire. A series of 1- and 3-year studies led to conclusions that ranged from fire increasing, not affecting, or decreasing ANPP in this grassland. Longer-term studies always resulted in statistically sound conclusions that fire increased ANPP, with maximum ANPP in sites burned infrequently. The results from these case histories demonstrate the need for: (1) long-term ecological research in fire ecology, and (2) studies that focus on the impact of fire frequency, not just the burned versus unburned state of ecosystems, in order to assess the ecological consequences of different fire management regimes.

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INTRODUCTION

Fire has been recognized as an important, and often an essential, ecological factor in a wide array of biomes (Daubenmire 1968, Ahlgren 1974, Pyne 1982). More recently, the management of prescribed fire in ecosystems previously protected from fire has become relatively common. However, the frequency at which prescribed fire should be imposed is less well understood primarily because studies of the long-term effects of different fire frequencies are few in number (Towne and Owensby 1984). Grassland ecosystems offer the unique opportunity to assess both the role of fire as a management tool and the long-term impact of how variation in fire frequency influences ecosystem structure and function. This is possible, particularly in the more productive tallgrass prairie ecosystems of the central United States, because sufficient fine fuel is produced each year to allow for an annual fire regime (Knapp and Seastedt 1986). Such a regime can then be compared to alternate fire frequencies (i.e., fire every 2, 4, 10, or 20 years) and to unburned grasslands, thus allowing for an assessment of a wide range of fire frequencies. Experimentally varying fire frequency by a factor of 20 in forested ecosystems is possible, but such studies would require several generations of scientists to complete.

The long fire-return interval that is characteristic of many wooded ecosystems is probably the primary reason why the implications of varying prescribed fire frequency are poorly known. Evaluating the effects of different fire regimes requires a long-term commitment to both the implementation of prescribed fire and the measurement of ecosystem responses. Nonetheless, there is ample evidence that such an evaluation is needed, given that differences in historical fire frequencies have been reported to have profound effects on grassland, shrubland, and forested ecosystems (Grimm 1984, Arno and Gruell 1983).

In this paper we present data from over 20 years of prescribed fire research at a tallgrass prairie site in northeastern Kansas, the Konza Prairie Research Natural Area. This site, a member of the National Science Foundation's Long-Term Ecological Research (LTER) Network, has implemented a fully replicated experimental design that explicitly incorporates a long-term perspective into the study of ecological phenomena (Callahan 1984). As a major component of the fire ecology research program at Konza Prairie, the LTER program has made a commitment to the evaluation of the long-term ecological consequences of varying fire frequency in this tallgrass prairie. Our goal for this paper is to present several case histories that: (1) demonstrate the value of long-term studies in fire ecology, and (2) assess the impacts of varying fire-return intervals in a grassland ecosystem.

ROLE OF FIRE IN GRASSLANDS

That fire has been an integral part of the evolution of grasses and grasslands worldwide is well-accepted (Axelrod 1985, Anderson 1990). Across the Great Plains of the United States, there is a strong west to east gradient of increasing precipitation, aboveground production (Sala et al. 1988), and fire frequency. Even though fire may have been less common in shortgrass or desert grasslands relative to the tallgrass prairies to the east, fire has been cited as being important throughout the region in maintaining both the dominance of the characteristic grassland flora as well as restricting fire-sensitive woody plants to locales such as escarpments or riparian zones that offered protection from fire (Wells 1965). In the tallgrass prairies of eastern Kansas, which border the eastern deciduous forests, frequent fires are essential for controlling woody plant invasion of these grasslands (Bragg and Hulbert 1976, Knight et al. 1994). As a result, fire is a commonly utilized management tool in this region.

STUDY AREA

The Konza Prairie (39° 05′N, 96° 35′W) is a 3487 hectare native (unplowed) tallgrass prairie site representative of the 50,000 kilometers^2 Flint Hills region of eastern Kansas. Alternating layers of Permian limestone and shale lie beneath soils that vary from deep (>1 meter) silty clay loams in lowlands to rocky shallow soils on ridges. Konza Prairie has a typical midwestern continental climate with warm, wet summers and cold, dry winters. Interannual climatic variability is high (Borchert 1950). Mean annual air temperature (30-year average) is 12.8°C with an average annual precipitation of 835 millimeters. The extremely variable climate, frequent fire, and grazing by large herbivores are all recognized as important factors in maintaining the structure of this grassland type (Borchert 1950, Axelrod 1985, Knapp and Seastedt 1986).

The flora of Konza Prairie is dominated by warm season (C_4 photosynthetic pathway) grasses including *Andropogon gerardii* and *Sorghastrum nutans,* but mid- and short-grasses, dominant in more arid grasslands, can also be found on sites with shallow soils. Over 300 species of forbs (nongraminoid herbs; almost all with the C_3 photosynthetic pathway) are found on Konza Prairie. Although the grasses dominate in biomass, it is the forb species that contribute most to plant species richness and diversity (Turner et al. 1995, Turner and Knapp 1996). Gallery forests (thin bands of forests along stream channels) are found throughout the site and are dominated by oak species (*Quercus macrocarpa* and *Q. muehlenbergii*).

Since 1972 in some areas, and since 1980 throughout the entire site, a watershed-level experimental design has been implemented to assess impacts of variation in fire frequency at Konza Prairie. This design includes replicated watersheds subjected to spring fires (April) at 1-, 2-, 4-, 10-, and 20-year intervals. Sites targeted for 20-year intervals between fire are considered unburned when compared to other fire frequency treatments. Grazing by large native ungulates (bison) also occurs on the site, but these herbivores have been reintroduced relatively recently. Thus, the data presented here will be for ungrazed sites. A wide variety of abiotic and biotic responses to these different fire frequencies are measured, but in this paper we will focus on responses in species richness and aboveground net primary production (ANPP) to illustrate the value of long-term ecological research and to evaluate

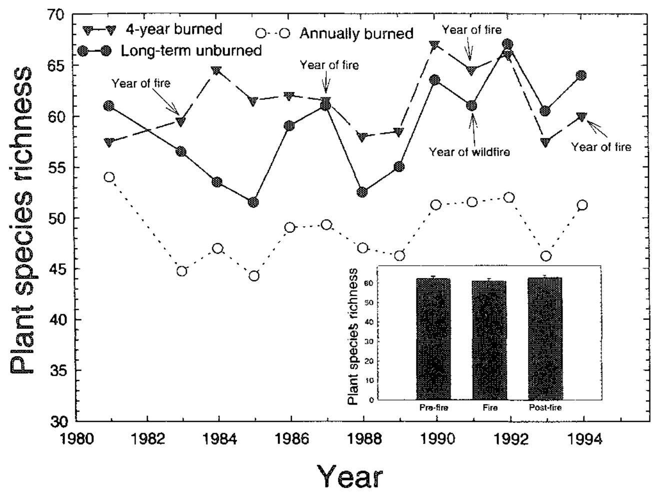

Fig. 1. Long-term record of responses to different fire frequencies in plant species richness from permanent transects in three different watersheds on Konza Prairie, northeastern Kansas. Community composition was determined at least two times each year by visual estimates of canopy coverage in 10 square meters circular plots in upland and lowland sites. In the watersheds not annually burned, the year of fire (including a wildfire) is indicated. Implementation of experimental fire treatments began at different times in the three watersheds in the mid-1970's through 1981, but prior to this time period all watersheds were exposed to a similar fire-grazing management regime. *Inset:* Pre- through postfire response of plant species richness to individual fires in those watersheds not annually burned.

the ecological consequences of different fire frequencies.

SHORT-TERM VERSUS LONG-TERM PERSPECTIVES

Species Richness

The 15–20 year data sets at Konza Prairie allow us to compare research results based on short-term as well as longer-term analyses of biotic responses to different fire frequencies. For example, from a short-term perspective, individual fires appear to impact plant species richness in tallgrass prairie in an inconsistent and nondirectional manner (Figure 1). Regardless of whether sites were burned at 4-year intervals or only once in 10 years, changes in species richness in response to individual fires (prefire, year-of-fire and postfire growing season comparisons) were not distinct from normal year-to-year variations. When these pre- through postfire responses were averaged for multiple fires, no response to an individual fire in species richness was noted (Figure 1). In contrast, when the two extremes of the fire frequency gradient imposed at Konza Prairie are considered (annual fire versus the unburned treatment) over a 15-year period, there were significantly fewer plant species in burned sites (Figure 2). Clearly, such cumulative changes would not be detected by short-term studies.

Plant community responses to the entire range of fire frequencies imposed at Konza Prairie have been

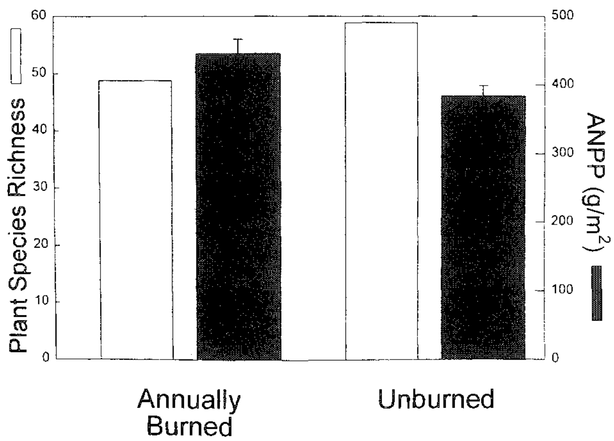

Fig. 2. Long-term average response in plant species richness (14 years) and aboveground net primary production (ANPP, 20 years) in watersheds burned annually or unburned (years after wildfires excluded). ANPP is estimated as peak aboveground biomass along permanent transects (methods in Briggs and Knapp 1995). ANPP is significantly higher, but species richness is lower, in burned versus unburned watersheds ($p>0.05$).

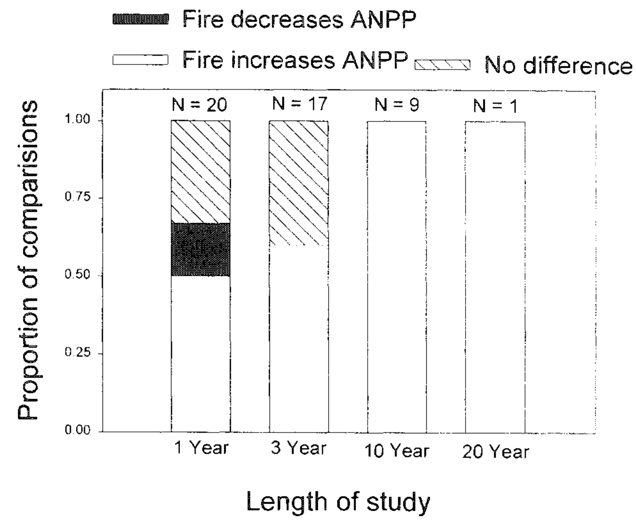

Fig. 3. Relationship between the length of study and the statistical results ($p>0.05$) of comparisons of aboveground net primary production (ANPP) in annually burned versus unburned watersheds. Analyses are from the 20-year record of ANPP responses to fire at Konza Prairie. Thus, there are 20 potential 1-year study periods for comparison, (17) 3-year study periods, (9) 10-year periods and (1) 20-year period. Only consecutive years were analyzed.

analyzed by Collins (1992) and others (Gibson et al. 1993, Collins et al. 1995). These researchers found that long-term exposure to intermediate (2–4 year) fire frequencies in this grassland often led to the greatest number of species and the highest plant species diversity (Collins and Wallace 1990). Thus, results from short-term (1–3 year) studies and those that do not incorporate a range of fire frequencies can lead to conclusions that vary from fire having no effect on plant species richness to fire decreasing plant species richness; both of which differ from the conclusions based on long-term experiments that incorporate a range of fire frequencies.

Aboveground Net Primary Production (ANPP)

Similar short- versus long-term comparisons can be made with responses of ANPP to fire and fire frequency. When ANPP is compared in burned versus unburned sites for periods of 1-, 3-, and 10-years, and for the entire 20-year period of annual fire versus fire exclusion, conclusions about the impact of fire on productivity differ substantially (Figures 2, 3). Indeed, the probability of concluding that ANPP was either not impacted or was decreased by fire in 1-year studies was 50%. Again, such conclusions would not be consistent with our long-term records which indicate that fire generally increases ANPP (Figure 2).

A long-term data set also is critical for evaluating the interactive effects of climate and fire on ANPP. In tallgrass prairie, interannual variability in ANPP is substantial (as much as 4-fold; Briggs and Knapp 1995) in part because ANPP is controlled by multiple limiting factors such as water, light, or nitrogen (Knapp and Seastedt 1986, Schimel et al. 1991, Seastedt and Knapp 1993). This contrasts with most semiarid and arid grasslands where a single factor, precipitation, strongly controls ANPP (Sala et al. 1988). At Konza Prairie, statistical significance of the relationship between annual precipitation and ANPP depends strongly on the length of the study. For example, in unburned lowlands, a 19-year record was required to establish a statistically significant relationship between ANPP and precipitation (Figure 4). In burned uplands, after 4 years of study, a significant relationship be-

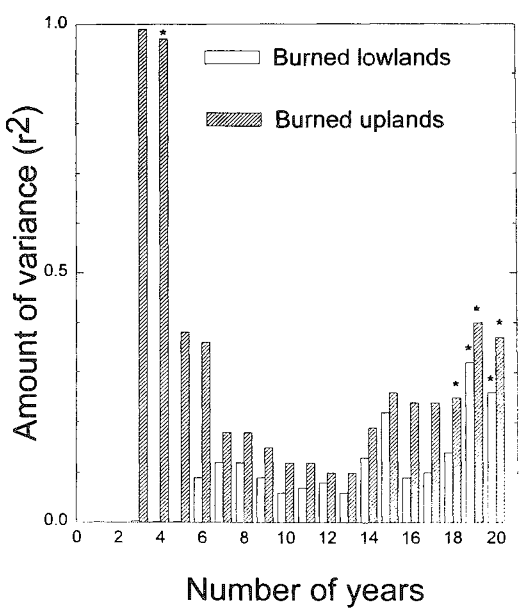

Fig. 4. The effect that the length of the data record has on the variance explained and the statistical significance of the relationship between aboveground net primary production (ANPP) and annual precipitation. Linear regression analyses were performed for consecutive years (from year 3 through 20) independently in upland and lowland locations. Statistically significant relationships are indicated by an "*".

tween ANPP and precipitation was detected with a relatively high amount of variability explained (Figure 4). Surprisingly, this relationship became nonsignificant as the study increased from 5 to 17 years, and only when the data set was extended to >18 years was the relationship reestablished (but with a much lower r^2; Figure 4). Again, these analyses illustrate the value of long-term studies of fire.

Studies of responses in ANPP to different fire frequencies (or time between fires) have shown that ANPP increases maximally after a fire in an infrequently burned site, and can be greater than ANPP measured in either annually burned or unburned sites (Briggs et al. 1994). This conclusion resulted from measurements made following a wildfire on Konza Prairie in 1991 that burned >30 watersheds, each with a different fire history. When ANPP was measured in these watersheds, ANPP was significantly higher (>200 grams/meter^2) in those sites that had been protected from fire for greater than 10 years compared to annually burned sites, which in turn were more productive than unburned sites (Briggs et al. 1994). Thus, from a long-term perspective, aboveground ANPP in tallgrass prairie is increased by annual fire relative to unburned sites, but maximum ANPP in any particular year occurs in sites exposed to fire frequencies intermediate between annual fire and fire exclusion.

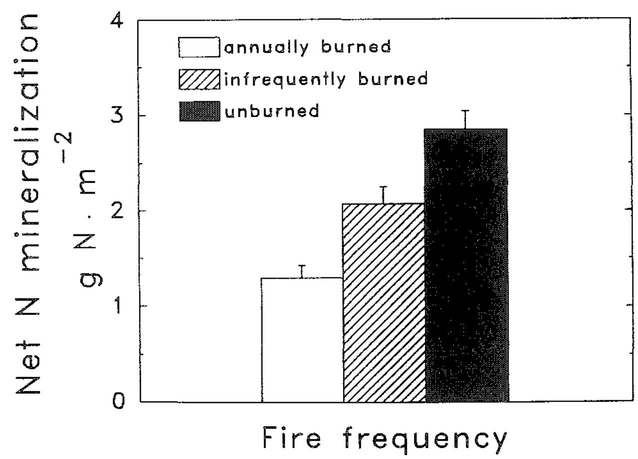

Fig. 5. Seasonal net N mineralization (May–Oct.), averaged over 2 years, in watersheds annually burned (spring fire for > 17 years), unburned (burned twice in 18 years) and infrequently burned (but burned in the year of measurement). Net N mineralization was greatest in the unburned sites, but remained significantly higher in the infrequently burned areas relative to those burned annually. Net N mineralization (0–15 centimeters) was measured at monthly intervals using the intact soil core technique (Raison et al. 1987).

MECHANISTIC BASIS FOR RESPONSES

Why do short-term versus long-term studies of fire often result in conflicting results? And what are the mechanistic bases for these unique responses in plant species richness and ANPP to intermediate fire frequencies? The former question may be answered most simply by recognizing that the flora of the tallgrass prairie is dominated by long-lived perennials that maintain their perennating organs belowground (Weaver 1954), thus minimizing potential direct negative effects of fire. Thus, responses to individual fires would be expected to be minor. Longer-term exposure to various fire frequencies, which may alter competitive environments (Turner and Knapp 1996), may be necessary before shifts in community composition result. In the long-term, tallgrass prairie that is annually burned provides a high light environment for plant growth; however, these sites become nitrogen-limited after several years of fire (Ojima et al. 1994). Additionally, in all but the wettest years, burned sites are more water-limited than unburned prairie (Knapp 1985, Knapp and Seastedt 1986, Seastedt et al. 1991). In contrast, unburned sites are light-limited, especially in the spring when the standing dead litter layer can intercept greater than 50% of the incoming solar radiation potentially available to emerging shoots (Knapp 1984). Unburned sites are seldom water-limited and show little response to nitrogen fertilization (Seastedt et al. 1991).

Reduced species richness in long-term annually burned sites is due to strong dominance by the C_4 grasses and reduced C_3 forb abundance (Collins and Wallace 1990). The high light, water, and nitrogen use efficiency characteristic of the grasses may provide them with a strong competitive advantage in such sites (Turner et al. 1995) and lead to high ANPP in burned sites. In contrast, increased species richness in unburned and infrequently burned sites reflects an increase in forbs, with maximal richness at intermediate fire frequencies. This is consistent with the intermediate disturbance hypothesis (Huston 1994). Many forb populations tend to respond positively to the unburned prairie environment of high nitrogen (Owensby et al. 1970) and reduced grass biomass (Briggs and Knapp 1995), but others may increase in burned sites (Towne and Knapp 1996). Thus, sites burned at intermediate fire frequencies may provide an environment with optimal resources and competitive interactions to maximize species richness (Collins and Wallace 1990).

The mechanistic basis for maximum postfire ANPP in sites burned at intermediate fire frequencies is a product of the multiple limiting factors operating in this grassland, and the disparate effects of infrequent fire versus annual burning on N availability (Ojima et al. 1994). Seastedt and Knapp (1993) argued that while frequently burned sites are nitrogen-limited, unburned sites, which are light-limited, may accrue soil N. When such a site is burned after a period of fire exclusion (>5 years), neither light nor nitrogen are limiting for at least one year. Hence, ANPP in such sites responds with maximum production, similar to annually burned sites that are fertilized. Recent measurements of *in situ* net nitrogen mineralization in sites subjected to a variety of fire frequencies are consistent with the hypothesis that strong interactions between nitrogen availability and fire frequency are key to understanding this ANPP response (Figure 5).

TOWARD THE FUTURE: CLIMATE CHANGE, FIRE FREQUENCY AND BIODIVERSITY

The results presented above need to be interpreted with the recognition that neither climatic regimes nor biotic responses are static over long time periods. Indeed, the role that fire frequency plays in determining plant species richness, which scales directly to biodiversity at a variety of trophic levels (Kaufman et al. 1990, Zimmerman 1993), and ANPP, which in grasslands may be related to diversity and community stability (Tilman and Downing 1994), will almost surely be altered by projected climate changes. Although predictions of global warming and precipitation changes are uncertain, especially in the Midwest (Karl et al. 1991), there is little doubt that atmospheric CO_2 concentrations will continue to increase through the next century (Easterling 1990). Over 7 years of experimentation with intact tallgrass prairie enclosed within open-top chambers at ambient or double ambient CO_2 suggests that this C_4-dominated system will respond to increasing CO_2 concentrations with increased ANPP in dry years (Owensby et al. 1993, 1995). This response is mediated by improved water relations (plant and soil) through high CO_2 induced reductions in stomatal conductance (Knapp et al. 1993, 1996, Ham et al. 1995). The C_3 species characteristic of this grassland have not increased in abundance in response to increased CO_2 and many are decreasing (Owensby et al. 1993). Thus, the net result of increased CO_2 is continued dominance by the warm season grasses and a likely lessening of the impacts of drought due to increased water use efficiency.

Such a scenario suggests that ANPP will be more stable from year-to-year and fire as a management tool may become even more frequent in tallgrass prairie in order to remove the previous year's litter layer and increase ANPP. Ultimately, such changes may lead to increased dominance by the C_4 grasses and reduced plant species diversity. Moreover, droughts, defined by the degree of water stress plants experience, will be less severe as atmospheric CO_2 increases. This may also decrease plant species richness in tallgrass prairie. Although Tilman and Downing (1994) found that more diverse grassland plots were less impacted by drought and recovered more rapidly than low-diversity plots, we have noted that two drought years in succession appear to have led to an increase in forb abundance at several sites across Konza Prairie (Figure 6), perhaps through a reduction in grass ANPP. Thus, elevated CO_2 has the potential to reduce plant species diversity through a variety of mechanisms. Since the establishment and maintenance of high biodiversity is often a management goal for both relict and restored tallgrass prairie sites (Samson and Knopf 1994, Howe 1994), fire frequency or the timing of fires may have to be altered, or grazing by large herbivores reintroduced, to shift the competitive balance from the dominant C_4 grasses to the more diverse C_3 forbs (Fahnestock and Knapp 1993, 1994, Hartnett et al. 1996).

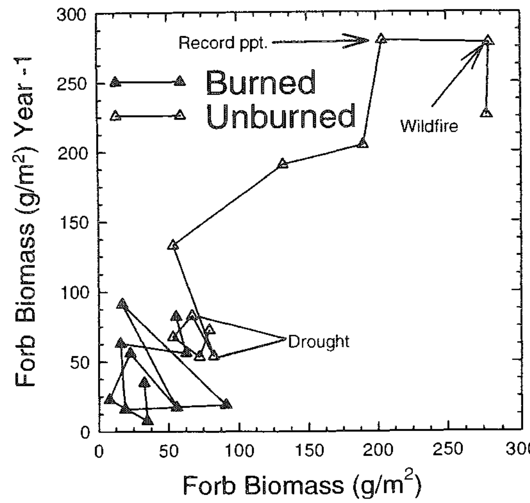

Fig. 6. Representation of year-to-year variability and directional trends in aboveground biomass of forbs (C_3 non-woody non-graminoids) in two adjacent watersheds, one annually burned and one unburned (except for a wildfire noted on the figure). Unusual climatic years are also noted. Consecutive drought years in 1988–89 appear to have differentially impacted forb populations in the unburned watershed (positive effect) versus the burned watershed (no effect).

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